

collecting data and observations. Dr. Glen M. Kohls kindly compared the material reported here with type specimens of *O. (A.) amplus*. Dr. M. G. R. Varma furnished a specimen from near the type locality; this may or may not represent the new species but points up to the frequent medical importance of argasids inhabiting breeding grounds of marine birds.

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MUESEBECKELLA, A NEW GENUS OF FLEA FROM NEW GUINEA, WITH NOTES ON CONVERGENT EVOLUTION¹ (SIPHONAPTERA: PYGIOPSYLLIDAE)

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ABSTRACT—*Muesebeckella*, n. gen., is described and illustrated on the basis of *M. mannae*, n. sp. and *M. nadi*, n. sp., both from *Pseudochirus* sp. in the mountains or foothills of the Territory of Papua and New Guinea. *Muesebeckella* is near *Striopsylla* Holland, 1969, and *Ernestinia* Smit, 1953, and the flattened head and spiniform or stout frontal bristles of all three genera of fleas are believed to be adaptive modifications for remaining on the host. Notes are included on convergent evolution and on structural developments on certain groups of Siphonaptera.

Scientists familiar with the multitude of significant contributions made by C. F. W. Muesebeck to the study of Hymenoptera may be surprised to see an article on Siphonaptera in a Jubilee Volume dedicated in his honor. It would seem that an entomologist who had accomplished so much in such a difficult field and who also nevertheless somehow managed to serve as an authority on the principles of taxonomy and on the standardization of common names of insects, could

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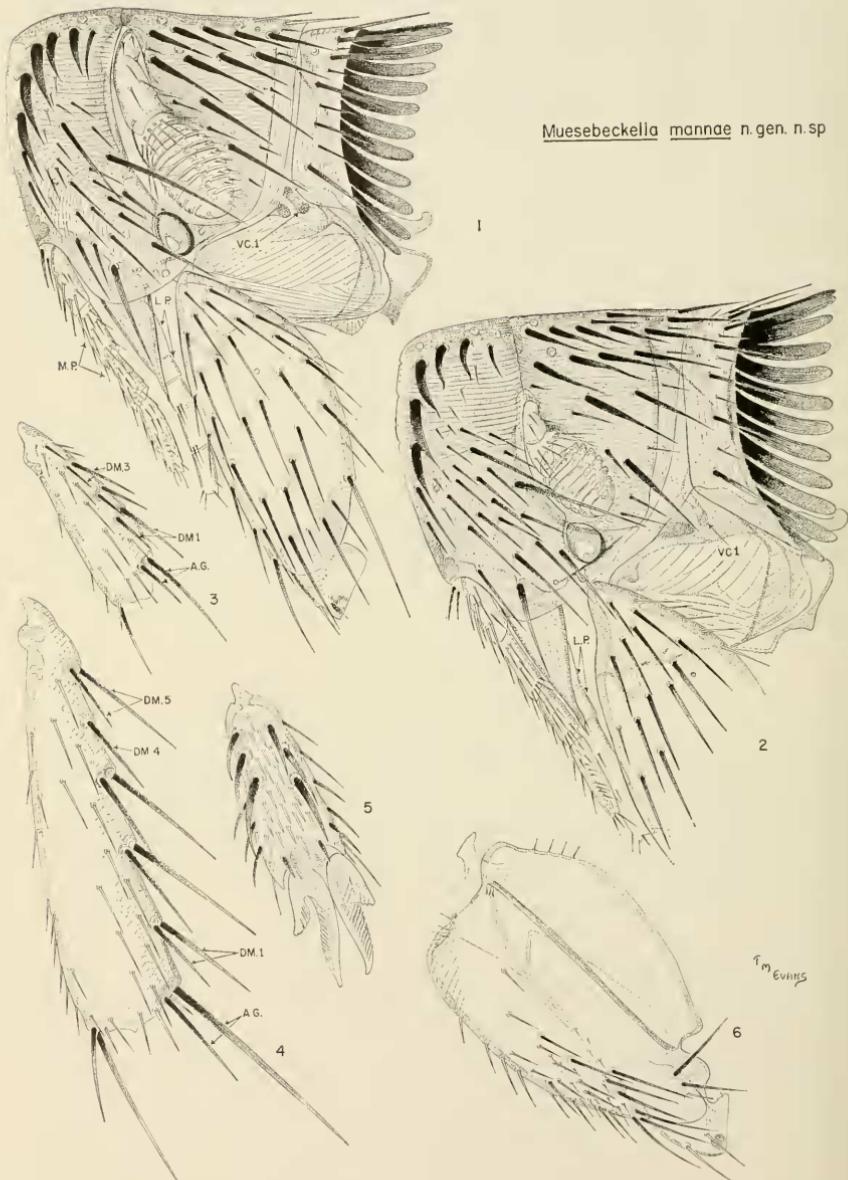
surely not find the time to master the systematics of fleas and lice. The fact is, however, that Mr. Muesebeck is expert enough on both of these groups of ectoparasites to have repeatedly provided definitive identifications of obscure species, despite the dearth of taxonomic keys, proper descriptions and illustrations for which at least the Siphonapteran literature is notorious. Even if this were not the case, it would be fitting to include a paper on fleas in this volume because of all that Mr. Muesebeck has done to stimulate students of ectoparasites and to ensure that the U. S. Department of Agriculture and the Smithsonian Institution would always be able to identify specimens and answer queries submitted from all parts of the world. When one considers the serious problems posed over the years by the shortage of funds to support such activities, the true value of Mr. Muesebeck's "extracurricular" activities becomes apparent.

The present article deals with the description of a new genus and two new species of marsupial fleas collected by the author and colleagues in New Guinea during studies of potential vectors and reservoirs of infection carried out by a joint team from the Department of Microbiology, University of Maryland School of Medicine (Baltimore) and the Bernice P. Bishop Museum (Honolulu). Notes on convergent evolution, illustrated by the new genus, follow the descriptive section.

Subfamily PYGIOPSYLLINAE
Muesebeckella, n. gen.

Near *Ernestinia* Smit, 1953, and *Striopsylla* Holland, 1969, in that the head is foreshortened and flattened and bears conspicuous longitudinal, parallel striae on the surface. Instantly separable from *Ernestinia* by the following: 1) Absence of the hooklike projection near the anterodorsal angle of the head. 2) Only the marginal bristles of the frons (figs. 1, 2) are subspiniform (shortened, thickened and darkly pigmented), while the remainder of those on preantennal region are unspecialized. In *Ernestinia* virtually all of these bristles are modified along the lines of spiniforms. 3) Male antepygidal bristles (fig. 8, A.B.) slightly displaced from dorsal margin and with the tergum produced into a lobe above their bases, instead of being dorsal and wholly marginal in position. 4) Movable finger (fig. 11) almost rectangular save for short stiva ("plow-handle") at apex, instead of with both margins diverging markedly subapically. 5) Male ninth sternum (fig. 12) lacking the tuft of long apical bristles of *Ernestinia* but possessing a "spanner-like" subapical structure which is absent in the other genus.

Readily distinguishable from *Striopsylla* as follows: 1) Head much more angulate, the anterior and dorsal margins almost straight and hence meeting at an angle of nearly 90° at level of origin of antenna,



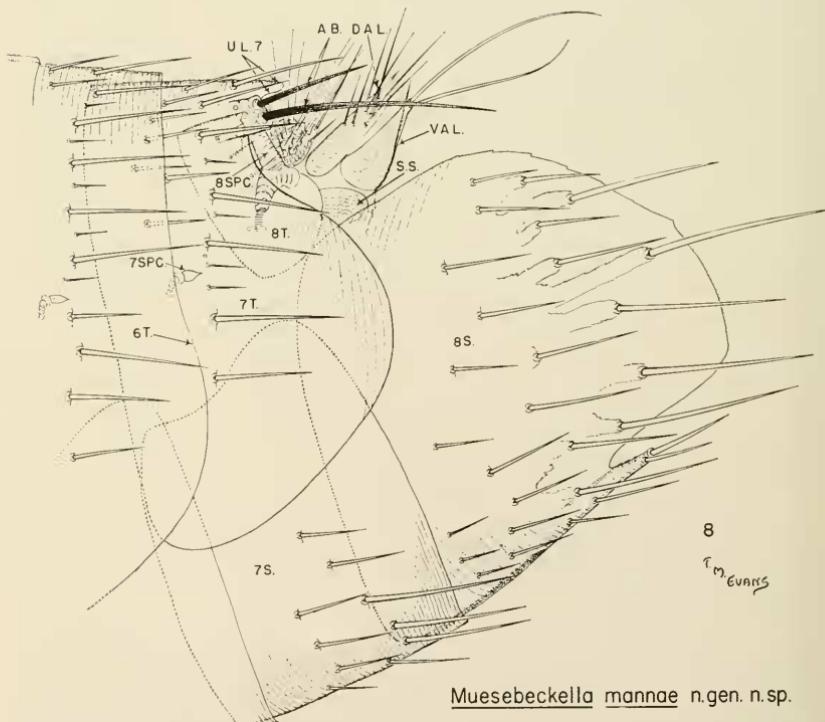
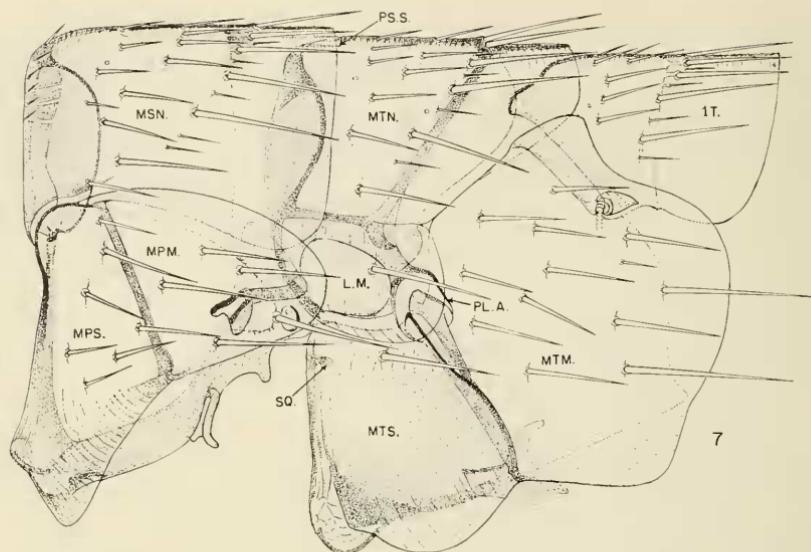
Figs. 1–6. *Muesebeckella mannae*, n. gen., n. sp.: 1, ♂ head and pronotum; 2, ♀ head and pronotum; 3, ♂ protibia; 4, ♂ metatarsus 5; 5, ♂ metacoxa.

instead of frons curving dorsad well below vertex so that only lower $\frac{2}{3}$ is sub-perpendicular. 2) First two rows of bristles of postantennal region virtually horizontal in position instead of oblique. 3) Head with an anteromarginal clear or unsclerotized area at upper third or half, and the margin itself is thin and presumably leathery and pliable in this region. These modifications absent in *Striopsylla*. 4) All but lower two of frontomarginal bristles of head definitely or strongly subspiniform instead of being only slightly so. 5) With a dorsal lobe above antepygidal bristles in both sexes (figs. 8, 23). These absent in *Striopsylla*. 6) Movable finger quite straight instead of being arched near base. 7) Female ventral anal lobe (fig. 19, V.A.L.) fairly close to body by virtue of short basal (anterior) stem; not clearly angulate and with basal stem at least half length of flap.

Generic Description: Caput integrecipit (figs. 1, ♂; 2, ♀). Frons relatively straight and vertical to top of head; dorsal margin of head also quite straight. Preantennal region much higher than long. First row of bristles of both parts of head submarginal and following outline of head; uppermost of those of pre-antennal region subspiniform; remaining bristles relatively unmodified. Eye somewhat reduced, placed far to rear, over base of forecoxa. Antennal segment 2 with bristles short in both sexes. Antennal groove not extending on to propleuron. Postantennal region with 3 complete rows of bristles. Labial palp (L.P.) 5-segmented, excluding palpiger, and not reaching beyond $\frac{3}{4}$ length of procoxa.

Prosternosome lacking a distinct sinus for receiving first vinculum (VC.1). Pronotum much narrower than length of spines of its comb, with one row of bristles. Procoxa fairly broad but not particularly squarish dorsally. Mesonotum (fig. 7, MSN.) with only a few pseudosetae. Pleural arch well sclerotized. Meso- and metacoxae with a few thin, scattered mesal bristles on ventral half. Profemur lacking thin, scattered mesal bristles; with a few such dorsal ones. Dorsolateral bristles in notches on posterior (outer) margin of tibiae largely paired (figs. 3, 4). Metatarsal segment 5 with 6 pairs of lateral plantar bristles, of which third pair is somewhat displaced towards mid-line (fig. 5). Some abdominal terga with a few apical spinelets. Unmodified terga very broad, extending ventrad to about middle of sternum; with 2 rows of bristles in ♂, 3 in ♀. Representative fossae of abdominal spiracles sagittate or lanceolate. Both sexes with 2 antepygidal bristles per side, with a dorsal lobe on seventh tergum (U.L.7), above plate of antepygidal bristles. Sensilium longer than arch is high; with 4 rows of sensory pits.

Male. Tergum 8 (fig. 8, 8 T.) very small, scarcely extending below spiracular fossa. Sternum 8 (8 S.) correspondingly very large, extending dorsad to base of anal lobes; with a conspicuous ventrocaudal sinus and a resulting narrow ventromarginal lobe. Manubrium (fig. 9, MB.) very broad (to near apex), more than 1.5 times as long as broad. Immovable process (P. and fig. 11) of clasper dorsally truncate, not produced into a lobe at dorsocaudal angle. Tergal apodeme of segment 9 (T.AP.9) subrectangular. Movable finger (F.) of clasper upright, digitoid in shape, only slightly expanded apically, hence lacking a true stiva ("plow-handle"). Fulcal sclerite (F.S.) higher than long (main axis vertical). Tergal apodeme of ninth segment (T.AP.9) somewhat longer than broad.



Muesebeckella mannae n.gen. n.sp.

Figs. 7-8. *Muesebeckella mannae*, n. gen., n. sp.: 7, meso-, metathorax and 1st abdominal tergum; 8, ♂ abdominal segments 6-8.

Proximal arm of ninth sternum (P.A.9) subrectangular. Distal arm of ninth sternum (D.A.9) with distal $\frac{3}{4}$ of subuniform breadth; with short apical and subapical marginal spiniform and with a biconvex submedian spanner-like sclerite. Aedeagal apodeme (fig. 10, AE.A.) relatively narrow. Middle lamina with its sinus or bay (B.M.L. and fig. 17) extending well anterior to fulcral area. Girdle of aedeagal pouch broad and with ventral margin well sclerotized. Hood (HD.) enclosing most of sides of endchamber; lateral lobes accordingly reduced, inapparent. Sclerotized inner tube (S.I.T.) horizontal, long, unmodified except for conspicuous ventral armature (V.AR.). Phylax (PHY.) present. Without a caudad-directed process on basal sclerite of crochet, i.e., lacking a true crochet. Ford's sclerite (F.SC. and fig. 17, ALPH., U.A., L.A.) very large, occupying most of apical portion of endchamber. Penis rods (P.R.) short, uncoiled. Y-sclerite (Y.S.) and lateral shafts of capsule (L.S.C.) relatively well sclerotized.

Female. Spermatheca (fig. 23, SP. and figs. 27, 28) with bulga (B.) much longer than broad and slightly longer than hilla (H.), with a dorsomarginal, short hump. Ventral anal lobe (fig. 19, V.A.L.) not conspicuously angulate. Anal stylet (A.S.) long and narrow. Caudal margin of eighth tergum biconcave.

The type of the new genus is *Muesebeckella mannae*, n. sp., described below.

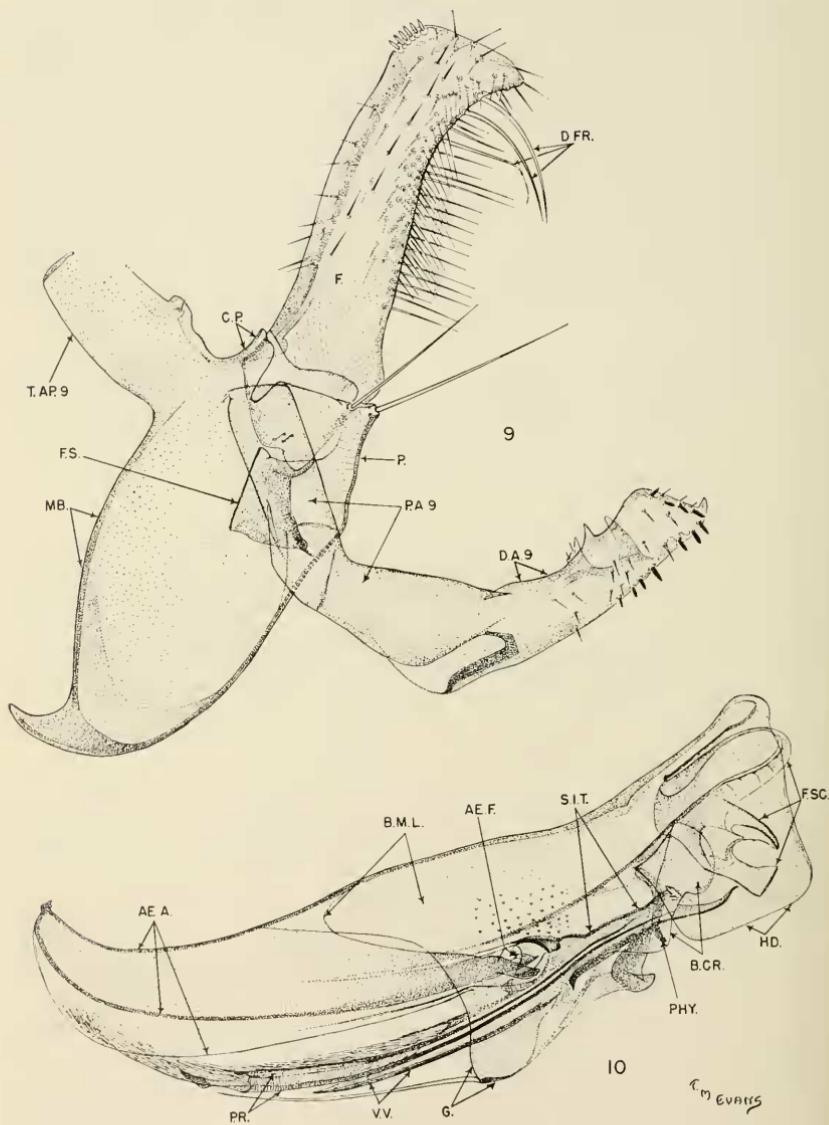
Comment. The genus is named for C. F. W. Muesebeck not only because of all he has done to advance the study of the systematics of insects in general and of arthropod parasites in particular, including Siphonaptera, Anoplura and Mallophaga, but also in recognition of his own significant knowledge of the taxonomy of these ectoparasites.

Additional comments on the genus follow the descriptions of the two new species below.

Muesebeckella mannae, n. sp.

Type Material. Holotype ♂ (slide #B-81015-1, with aedeagus in lateral position mounted on same slide but under separate cover-glass) ex a small species of ring-tailed possum, *Pseudocheirus* sp.; New Guinea: Papua, Southern Highlands, Mt. Giluwe, Kagaba, 40 km. NNE of Mendi; elev. 2800 m.; Coll. R. Traub; 17.IX.1968. Allotype ♀ (B-83160) ex same species of host; loc. cit.; Coll. M. Nadchatram & A. B. Mirza; 21.XII.1967. Paratypes: 4♂, 2♀ with same data as holotype (B-81015-4 with dissected aedeagus mounted dorsally; B-81015-2, ventrally); 1♂ ex same host but Western Highlands, Hagen Sub-district, near Mur Mur Pass, 16 km. NNE of Tambul; Coll. R. Traub & E. B. Mann; 7.X.1968. Holotype (U.S.N.M. #70747) and allotype in U.S. National Museum, Washington, D.C.; paratypes in Canadian National Collection and that of author.

Diagnosis. The shape of the components of Ford's sclerite, the lack of striae on the aedeagal hood, the shape of the distal arm of the ninth sternum and the chaetotaxy of the movable process of the clasper are all diagnostic, as are the shape of the anal stylet of the female and that of the spermatheca. These are



Muesebeckella mannae n.gen. n.sp.

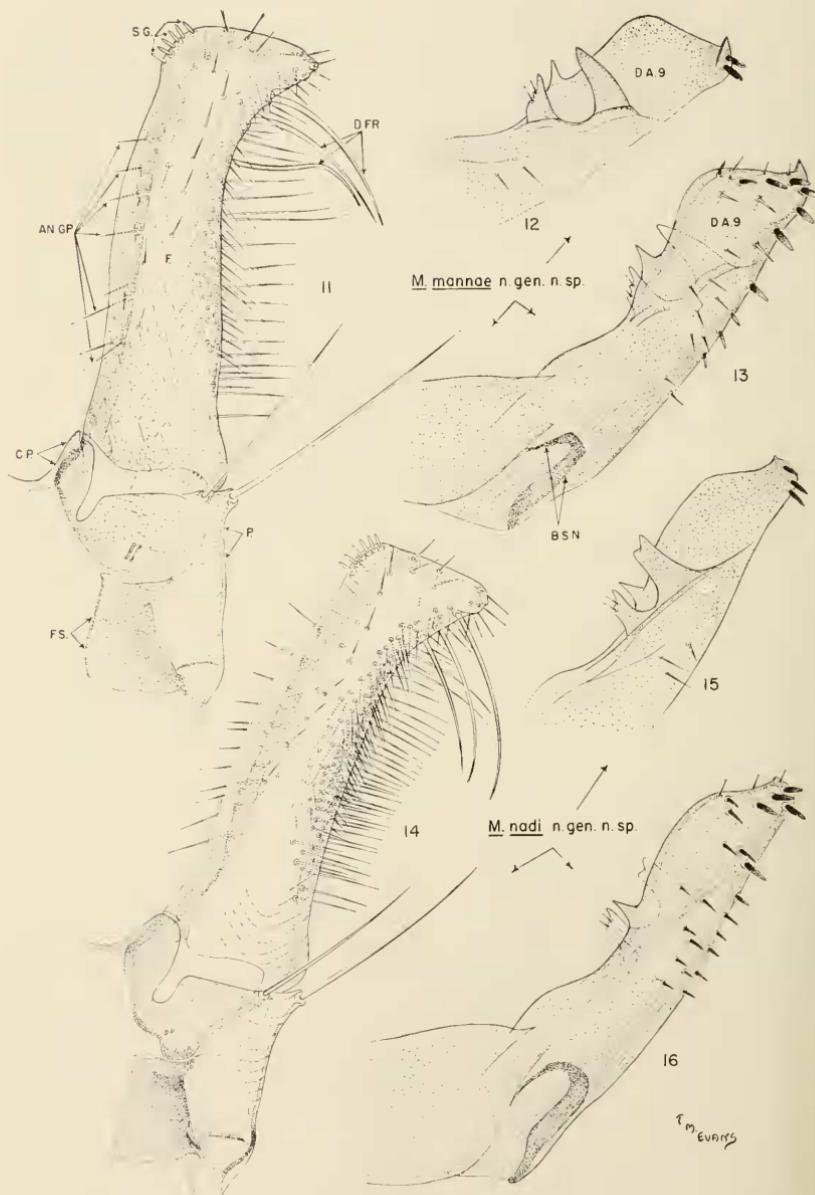
Figs. 9-10. *Muesebeckella mannae*, n. gen., n. sp.: 9, claspers and 9th sternum; 10, aedeagus.

described in detail below and critically compared with those of the second new species in the description which follows.

Head. (figs. 1, ♂; 2, ♀). Head squarish; frontal and dorsal margins meeting at almost right angle and virtually at level of vertex; upper half of frontal margin nearly perpendicular and lower half only very slightly curving ventrocaudad; dorsal margin virtually straight and horizontal. Preantennal region about twice as high as long. Upper half of frontal margin only lightly sclerotized, apparently leathery and pliable; with a distinct clear area beyond it, extending to near bases of first row of bristles. Parallel cuticular striae or rugae on upper half of preantennal region and virtually all of postantennal region. First row of 8 bristles; frontomarginal, and following angle of head; bases of upper 3 in a horizontal line, paralleling top of head; lower 5 in subvertical row. Upper 3 of vertical group and first 2 of horizontal group definitely spiniform—i.e., dark, shortened, basally thickened and curved. With 17–20 additional bristles in 3–4 irregular rows (the higher numbers in ♀). Four of these long, viz.: 1) median, at level of lowest spiniform, 2) bordering middle of antennal groove, 3) in front of eye, and 4) ventromarginal above maxillary lobe. Eye fairly small; subvertical axis oblique and well exceeding horizontal. Genal process narrow but unspecialized. Maxillary lobe not reaching apex of third segment of labial palp but extending beyond third segment of maxillary palp (M.P.), the first 3 segments of which are subequal and shorter than apical one. Labial palp 5-segmented with apical 2 longer than preceding 2; not shorter than $\frac{3}{4}$ of procoxa. Antennal segment 2 with apical bristles scarcely reaching third joint of club. Postantennal region with 3 rows of fairly stout bristles and an additional extra long one near antennal fossa, between last 2 rows.

Thorax. Pronotum narrow, its length slightly more than half that of spines in comb; with 1 row of bristles. Pronotal spines about 24 in number; extending far down on pronotum, the lower 2 inserted at or near level of vinculum and obscuring its base; all but ventral 2–3 spines slightly concave dorsally, and the ventral ones quite straight; axis of all but dorsal and subdorsal spines inclined somewhat ventrocaudad (despite slight arch of spines), the ventral ones the most oblique and these inclined at angle of about 45° from horizontal; apices of all fairly rounded; of uniform width to near apex; median spines slightly more than 5 times as long as broad at middle. Mesonotum (fig. 7, MSN.) with 3 rows of bristles; the first abbreviated; with 2 subdorsal pseudosetae (P.S.S.) per side. Mesepisternum (MPS.) usually with an oblique row of 5 bristles and 1 dorsomarginal one below midline; at times with an additional submedian one near latter (as in figure). Mesepimere (MPM.) with bristles arranged 2-2-1; last by spiracular fossa. Metanotum (MTN.) with 3 rows of bristles but first very incomplete; lacking apical spinelets. Lateral metanotal area (L.M.) longer than high (measuring true margins); dorsal margin quite straight and horizontal; with 1 bristle, near ridge above well sclerotized pleural arch (PL.A.), which is higher than long. Metepisternum (MTS.) with 1 long subdorsal bristle. Squamulum (SQ.) about twice length of adjacent sclerotized margin. Metepimere (MTM.) with about 13–16 bristles in ♂ and 15–18 in ♀ in 3–4 irregular rows. Spiracular fossa of MTM. sagittate but fairly broad.

Legs. Metacoxa (fig. 6) with a median, vertical group of short, thin mesal bristles in 2 or 3 irregular rows on lower half, extending to anterior margin near apex. With 3–6 small, thin lateral non-marginal bristles scattered over profemur.



Figs. 11-13. *Muesebeckella mannae*, n. gen., n. sp.: 11, processes of clasper; 12, distal arm of ♂ 9th sternum; 13, distal arm of ♂ 9th sternum, mesal aspect. Figs. 14-16. *M. nadi*, n. gen., n. sp.: 14, processes of clasper; 15, distal arm of ♂ 9th sternum; 16, distal arm of ♂ 9th sternum, mesal aspect.

Meso- and metafemora with 2-3 dorsal submarginal, and 3 subapical, lateral bristles; remainder marginal, including 2 or 3 large ventral ones near apex. Protibia (fig. 3) with 3 pairs of dorsomarginal bristles (DM.1-DM.3); the "apical group" (A.G.) displaced somewhat proximad; 2 in number. Metatibia (fig. 4) with 2 bristles in apical group and 5 groups of dorsomarginals in notches (DM.1-DM.5) of which DM.4 is single. None of bristles of tarsi extending to or near apex of following segments; only a few even reaching middle of next segment.

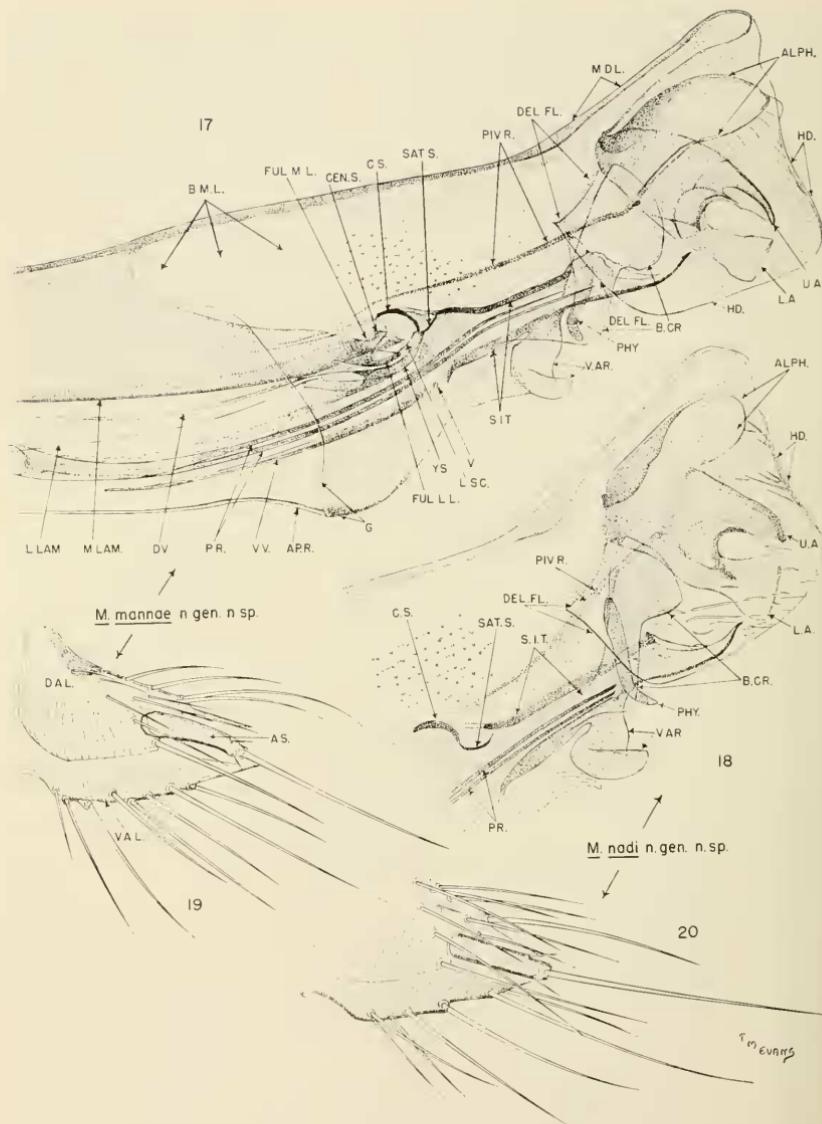
Measurements (in micra) of tibiae and tarsal segments (petiolate base excluded) for holotype:

Leg	Tibia	Tarsal Segments				
		I	II	III	IV	V
Pro-	188	50	50	42	40	88
Meso-	302	100	78	61	42	105
Meta-	422	307	210	122	75	105

Tarsal segment V with first pair of lateral plantar bristles slightly displaced towards midline; third pair somewhat more so (fig. 5, metatarsus ♂); subapical median spiniform plantar bristles usually as follows: ♂ 3-3(4)-2, ♀ 2-2-2.

Abdomen. Tergum 1 (fig. 7, 1 T.) shorter than preceding notum; with 2 rows of bristles preceded by 1-2 subdorsals. Basal sternum in ♂ with 2 or 3 small, thin ventromarginal bristles but no true median ones (these represented only by scattered microhairs or their bases); in ♀ with about 10 small, scattered median, lateral bristles, often in vertical groups of 2; plus 1 subventral and a well developed ventromarginal one. Terga 2-5 with 1 subdorsal apical spinelet per side. Unmodified terga in ♂ with first row not reaching spiracular fossa; caudalmost row with 3 bristles ventral to fossa and these lacking intercalaries, and usually with 1 small intercalary type immediately above and below fossa. In ♀, these terga with second row reaching near spiracular fossa; row shorter; last row usually with 2 small intercalaries between first 2 of group of 3 below fossa and a tiny one between lowest pair. Typical sterna in ♂ with 2 short rows of bristles; these preceded by a group of about 2 subventrals; ♀ with an additional short row. Upper antepygidal bristle in ♂ about half length of lower (fig. 8, A.B.); in ♀ (fig. 23, A.B.), slightly longer. Lobe above antepygidal bases (U.L.7) in ♂ twice as long as broad; in ♀, about as long as broad at base.

Modified Abdominal Segments—Male. Tergum 8 (fig. 8, 8 T.) about half as long as high (broad); extending ventrad only to level of base of ventral anal lobe (V.A.L.); devoid of bristles. Spiracular fossa 8 usually obscured by contiguous or overlapping sensilium; horizontal (oblique) section rather flaring, narrowing towards trachea, about twice as long as broad at middle; vertical portion nearly twice length of horizontal and half as broad. Sternum 8 (8 S.) very large, overlapping base of V.A.L. extending cephalad to cover about half of manubrium or to level of antepygidal bristles (A.B.); somewhat longer than high at maximum (middle) axes; anterior and posterior margins converging so that true dorsal margin about $\frac{1}{3}$ length of subventral portion; cephalic margin curving gradually; caudal margin shallowly microcrenulate, markedly convex for upper half, then fairly straight and vertical and then becoming sub-horizontal, running due cephalad so that it is excised subventrally, and at times deeply so, the sinus often narrow, straight and, ventrally, slightly more than twice as long

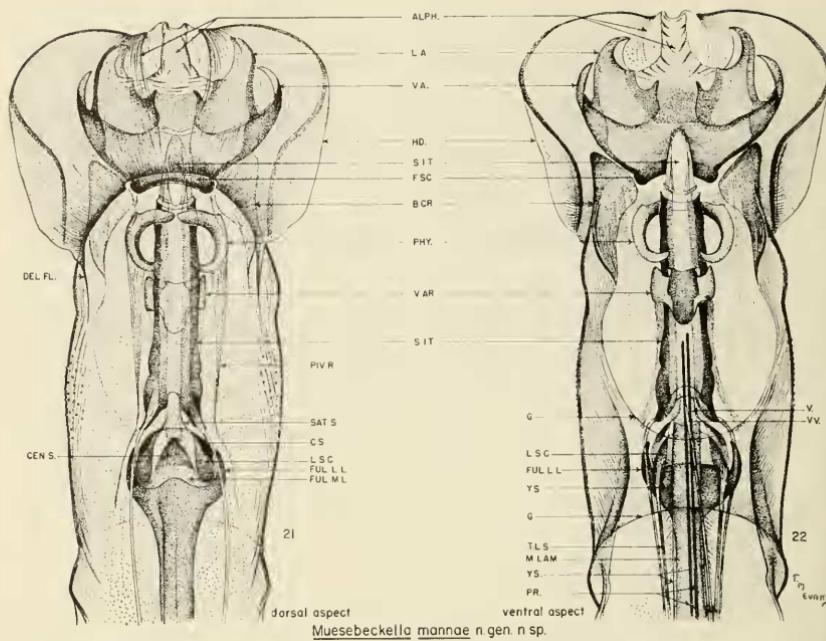


Figs. 17 & 19. *Muesebeckella mannae*, n. gen., n. sp.: 17, apex of aedeagus, lateral; 19, ♀ dorsal and ventral anal lobes. Figs. 18 & 20. *M. nadi*, n. gen., n. sp.: 18, apex of aedeagus, lateral; 20, dorsal and ventral anal lobes.

as broad. Lobe below sinus arising from ventral margin; narrow and straight, about 5–6 times as long as broad, and extending well anterior to sinus; bearing 1 or 2 stout apical bristles; remainder of ventral margin mildly sinuate. 8 S. clothed

with 3 rows of bristles, the rows curved and extending from subdorsal region to ventral, and caudalmost row with alternate (and large) bristles deeply displaced cephalad; in addition with 2 subventral short rows of small bristles anterior to these; with 4 or 5 ventromarginal bristles. Immovable process of clasper (figs. 9, 11, P.) dorsally straight and sub-horizontal; with a subapical dorsal bristle and a longer apical one arising from a short projection; caudal margin slightly sinuate and subvertical. Conical process (C.P.) of P. apically broad and concave; nearly twice as long (high) as broad. Movable finger (F.) with portion distad of P. nearly 4 times as long (high) as broad at middle; nearly vertical and almost straight, the sigmoid effect minimal; scarcely narrowing from base to near apex; stiva at caudodistal region only slightly developed, i.e., apex is only 1.3 times breadth of middle of F. Distal fringe (D.F.R.) usually consisting of 3 relatively thin bristles on apical fifth, uppermost of which is subapical. F. with thin bristles clothing caudal margin from near base to apex; some of these long; with about 3 rows of mesal thin, longish bristles bordering caudal margin, commencing at about basal fourth, the rows becoming single near apex, with a group of scattered submedian lateral bristles on apical half and similar but mesal bristles on anterior third. Anterior group (AN.GP.) of mesal marginals widely spaced and thin, submarginal. Sensilla-group (S.G.) consisting of 4-6 short, thickened bristles at anterodistal curve. With a pair of unequal, short, vermiform sclerotizations, suggestive of glandular or sensory structures near base of F. just above bulge resting on fulcral sclerite (F.S.), which, in turn, is about twice as long (high) as broad at middle and which is proximally broader than subapically due to slope of ventral half of caudal margin. Manubrium (MB.) massive; about 1.6 times as long (high) (measured from ventral margin of tergal apodeme of ninth segment (T.AP.9)) as broad at middle; only gradually narrowing to near apex, which is subacute and upturned; anterior margin shallowly convex to near apex; middle half of caudal margin quite straight. T.AP.9 about twice as long as broad; ventral margin slightly convex; dorsal margin with a subproximal, truncate, short bulge. Sternum 9 with proximal arm (P.A.9) angled somewhat ventrad of middle, and subequal to distal arm (D.A.9 and figs. 12, 13). Upper portion of P.A.9 subrectangular, about twice as long as broad; apex straight. D.A.9 relatively subrectangular but with dorsal margin bisinuate at apex (the lobe between the arcs acute) and distal margin sloping and terminating in a falcate projection at ventral angle; about 5.6 times as long as broad at level of trough of first sinus; with 2 spiniforms at base of apical projection and 2 or 3 spiniforms near distal margin; ventrally with 2 subapical spiniforms and 3-4 marginal ones at third quarter, of which most distad is nearly as large as those at apex; with conspicuous spanner-like, bilobed, mesal sclerotization (fig. 13, mesal aspect) extending obliquely from first dorsal sinus to near ventral margin; first such bulge with sinuate dorsal (anterior) margin bearing 2 small bristles and apical lobe longer, more acute; with a few scattered lateral bristles and about 3 small apicom marginal ones. D.A.9 with internal basal sclerotized notch (B.S.N.) fairly truncate apically and about $\frac{1}{5}$ of arm in length; the sinus about 4 times as long (measured ventrally) as broad at level of end of marked dorsal tanning.

Aedeagus-Lateral Aspect. (figs. 10, 17). Apodeme (AE.A.) with middle lamina (fig. 17, M.LAM.) more tanned than lateral laminae (L.LAM.); former about 4 times as long (from base of aedeagal fulcrum, AE.F.) as broad at edge of bay of middle lamina (B.M.L.) and gradually narrowing; apex somewhat



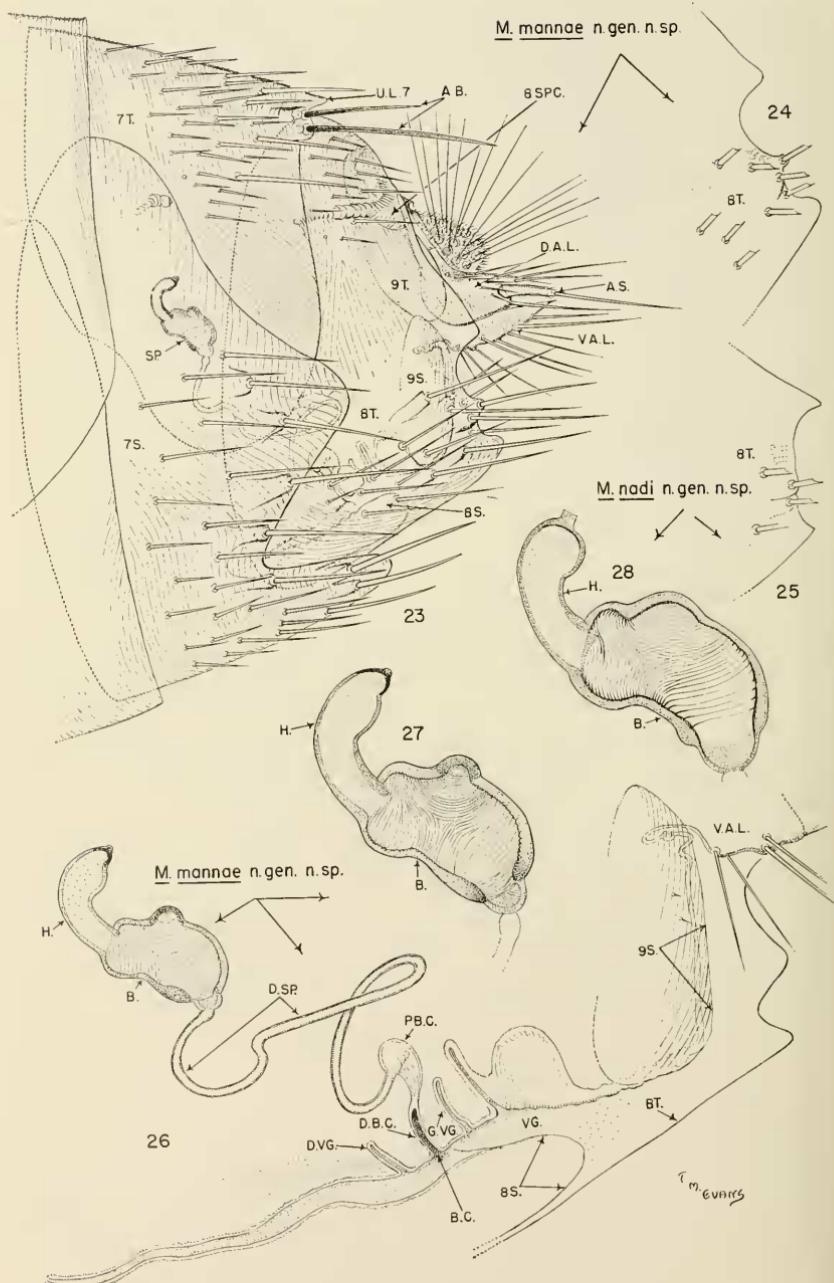
Figs. 21-22. *Muesebeckella mannae*, n. gen., n. sp.: 21, dorsal aspect of apical region of aedeagus; 22, ventral aspect of apical region of aedeagus.

upturned but rounded. Lateral laminae with ventral margin quite straight to near apex, where broadly rounded. B.M.L. extending cephalad more than half length of entire aedeagus. Median dorsal lobe (M.D.L.) fairly straight to level of phylax (PHY.) and then sloping dorsad gradually (about 30°). Girdle of aedeagal pouch (G.) conspicuous, well tanned and broad; its sclerotized ventral margin slightly longer than crescent sclerite (C.S.). Most of apical region of aedeagus enclosed by folds of well developed hood (HD.) which extends caudad to level of phylax as the deltoid flap (DEL.FL.) (which is much more obtuse than in some other taxa). Lateral lobes (L.L.) undeveloped. Ford's sclerite massive, dominating endchamber, its alpha portion (ALPH.) of F.S.C. with length exceeding maximum vertical diameter of middle lamina. ALPH. about twice as long as broad resembling a rounded "A" without the crossbar; ventrocaudal margin broad, fluted and sinuate and broadest at base. Securifer (SEC.) of F.S.C. subequal to ALPH. in length, spanner-like or chelate in appearance; with upper arm (U.A.) falcate and lower member (L.A.) somewhat apically broadened and truncate. Pivotal ridge (PIV.R.) rod-like. Sclerotized inner tube (S.I.T.) more than 7 times as long (measured ventrally) as broad at anterior fourth; ventrally with apical margin extended and somewhat upcurved; medially somewhat constricted, the posterior bulge occurring immediately before dorsal margin curves and narrows toward acuminate and ventral apex; at apical third with a large ventral armature (V.AR.), which is lobate and somewhat curved, its girth subequal to that of S.I.T. and its length (unextended) nearly twice its diameter.

Crescent sclerite (C.S.) shallowly convex, its length equal to breadth of S.I.T. Satellite sclerite (SAT.S.) short and weakly tanned. With a long, tendon-like structure of unknown homology and function entering dorsal portion of base of S.I.T. from behind C.S.; these extending well cephalad into apodeme. Fulcral lateral lobe (FUL.L.L.) relatively narrow and short, ovate. Central sclerite (CEN.S.) approximating fulcral medial lobe and accentuating its semi-sagittate appearance. Y-sclerite (Y.S.) prominent as an irregular dark sclerite below and behind capsule, arising from dorsal virga (D.V.). Lateral shafts of capsule (L.S.C.) well tanned. Phylax (PHY.) a fairly elongate sclerite flanking S.I.T. where posteriorly narrowing; shaped like an inverted and reversed sigmoid. Basal sclerite of crochet (B.C.R.) weakly tanned, with dorsal half of caudal margin convex; extending from base of F.S.C. ventrocephalad to base of PHY.; about thrice as high as long at middle; lacking any crochet-like caudal process. Vesicle (V.) weakly developed. Penis rods (P.R.) short and thick, scarcely reaching anterior third of apodeme. Aedeagal apodemal rod (AP.R.) continuing cephalad from ventral margin of girdle (G.). Ventral virga (V.V.) well developed, short.

Aedeagus-Dorsal and Ventral Aspects. (figs. 21, 22). Ford's sclerite bilaterally symmetrical but with components (ALPH., L.A., U.A.) fused along midline, hence not true pairs, and left and right members unable to move independently. Securifer with lobes falcate, directed mesad. Deltoid flap (DEL.FL.) with highly acuminate, apical (anterior) extensions. (These inapparent in lateral aspect.) Crochet lacking a caudad-directed arm and hence true crochets absent. Phylax (PHY.) curving around S.I.T. and almost meeting dorsally; more widely separated below S.I.T. Ventral armature (V.AR.) of S.I.T. with a ventral lobe. Pivotal ridge extending from base of Ford's sclerite far down to near apex of apodeme. Pouch walls beaded at level of fulcrum and basal third of S.I.T. Girdle (G.) continuing distad as pouch wall, which fuses with side of basal sclerite of crochet (B.C.R.). Lacking even a vestige of a caudal process or "paramere" on B.C.R. Y-sclerite (Y.S.) huge, flooring capsule of fulcral area; bifid, one fork enclosing much of distal part of capsule. Lateral shafts of capsule (L.S.C.) very large, their tendons (T.L.S.) somewhat sclerotized.

Female. (fig. 23). Sternum 7 (7 S.) about 1.6 times as high as long at maximum diameters, anterior margin nearly vertical; caudal margin bisinuate, the median lobe long, broad and rounded; the ventral lobe evenly narrowed; upper sinus shallow; lower sinus with dorsal margin virtually straight and at 45° angle, ventral margin horizontal. Sternum 7 with 3 main, uneven rows of bristles, of which caudalmost follows contour of sternal margin and hence highly irregular, and consisting of longest bristles; rows with approximately 7-9(8)-9(6)-8 bristles respectively, last row with 2 of these placed medially in ventral sinus and one anterior ventromarginal; with 3 subventrals preceding last-named and one ventromarginal between first 2 rows. Tergum 8 (8 T.) with caudal margin markedly biconcave below middle (fig. 24); upper sinus evenly and broadly ovate; lower one subventral, short, almost semicircular; lobe between the two small, its length about half its height at base; ventral lobe evenly rounded. Chaetotaxy of 8 T. approximately as follows: with 2 irregular rows of 6 and 5 short, thin bristles preceding spiracular fossa (8 SPC.); of these 2 below but near fossa; with a subventral row of 4 long lateral bristles; a group of 2 such bristles near caudal lobe; 8 additional submedian bristles on lower third of tergum, of which one or 2 are near caudal margin; with a group of 2 longish



mesal bristles above caudal lobe and 1 below it. Dorsal anal lobe (D.A.L. and fig. 19) with 3 long dorsomarginal bristles; about 5 smaller, thinner subdorsals, 2 submedian, and 1 at ventrocaudal angle below anal stylet (A.S.), which is slightly arched ventrad and about 5 times as long as broad at middle and bears 2 very small subapical setae, viz., 1 above and 1 below very long apical bristle; stylet broadest subproximally. Ventral anal lobe (V.A.L.) with very short ventral (basal) margin; essentially a fairly oblique, narrow structure fringed with about 8 long, thin, relatively well spaced bristles.

Spermatheca (SP. and figs. 26, 27) with bulga (B.) somewhat barrel-shaped except for marked dorsal bulge at anterior third; bulga otherwise of nearly uniform breadth most of its length; hilla (H.) about $\frac{3}{4}$ length of bulga, upcurved, subapically dilated caudally (dorsally), proximally about $\frac{2}{5}$ as broad as anterior part of bulga; with a sclerotized apical papilla. Bursa copulatrix (B.C. and fig. 26) only lightly sclerotized; perula (P.B.C.) subpyriform; duct (D.B.C.) feebly tanned. Duplicatura vaginalis (D.V.G.) and glandula vaginalis (G.V.G.) straight and relatively long. With a longer glandular structure of unknown homology caudad of latter, and preceding a large structure, paired, and ill-defined in mounted material, but terminating ventrally at the thickened dorsal apical wall of the genital opening.

Comment. The species is named for Miss Elizabeth B. Mann, Parasitologist at the Medical College, Port Moresby, who was an invaluable member of our 1968 expedition in New Guinea and cheerfully participated in all phases of the field-program despite the difficulties inherent in such operations in remote areas.

Muesebeckella nadi, n. sp.

Type Material. Holotype male and allotype female (B-81480-3) ex a small species of *Pseudocheirus* sp., a ring-tailed possum; Northeast New Guinea, West Sepik District, Oksapmin, Strickland River, near northern border of Western District of Papua; elev. 1850 m.; Coll. R. Traub; 24.X.1968. Paratypes: 7♂ and 2♀, ibid.; 1♂ and 1♀ ibid., but 19.X.1968 (B-81430). (The first possum had been collected together with its mossy nest in a small tree, and 5♂ and 2♀ of the paratypes were subsequently reared from the nest-material.) Holotype and allotype deposited in U.S. National Museum, Washington (U.S.N.M. #70748); paratypes in Canadian National Collection, the Rothschild Collection of Fleas at the British Museum (Natural History) (Tring), and that of the author.

Diagnosis. Close to *M. mannae* n. sp., but separable as follows: 1) Distal arm of ninth sternum (figs. 15, 16) with apical region narrower and excised dorsally instead of slightly broadening subapically and being subtruncate at tip (figs. 12,

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Figs. 23, 24, 26, 27. *Muesebeckella mannae*, n. gen., n. sp.: 23, ♀ modified abdominal segments; 24, ♀ sinuses of 8th tergum; 26, internal ♀ genitalia; 27, spermatheca. Figs. 25 & 28. *M. nadi*, n. gen., n. sp.: 25, ♀ sinuses of 8th tergum; 28, spermatheca.

13, *M. mannae*). 2) Most apical of mesal lobes on D.A.9 bifurcate instead of acuminate. 3) Securifer with upper arm (fig. 18, U.A.) broader and subtruncate, instead of falcate (fig. 17, U.A.), and lower arm (L.A.) proportionately shorter; broader and less angulate apically. 4) Hood of aedeagus (HD.) bearing scattered short cuticular ridges or striations; these absent in *M. mannae*. 5) Movable finger (fig. 14, F.) clothed with more numerous small mesal setae near caudal margin, viz., 4 non-marginal rows in central portion, not 2 or 3 (fig. 11, F.). 6) Narrow ventrocaudal lobe of male eighth sternum elongate—7 or 8 times as long as broad (fig. 8), not 5–6. 7) Anal stylet straight and sides virtually parallel throughout (fig. 20, A.S.) instead of being somewhat arched and broadest near base (fig. 19, A.S.). 8) Sinuses and small lobe on lower half of caudal margin of female eighth tergum (fig. 25) not as large nor as symmetrical as in *M. mannae* (fig. 24). 9) Spermatheca (fig. 28) with hilla (H.) subglobular at apex, not ovate (fig. 27, H.).

In other respects, *M. nadi* n. sp. is essentially like *M. mannae* and hence is not described in detail.

Comment. The species is named for my colleague and good friend, M. Nadchatram, Acarologist of the Institute for Medical Research, Kuala Lumpur, Malaysia, currently seconded to the Bernice P. Bishop Museum at Honolulu. Nad, as he is known to all of us, not only is an outstanding worker on ectoparasites in his own right, but by virtue of his collections in Malaysia, Nepal, North Borneo, Laos and New Guinea, he has greatly enhanced our knowledge of parasitic insects and acarines. Through his field-work in New Guinea in particular, both as a member of our team and as leader of the one earlier in the year, he has tremendously contributed to our understanding of the Siphonapteran fauna.

COMMENT ON THE GENUS *Muesebeckella* AND NOTES ON CONVERGENT EVOLUTION

The genus *Muesebeckella* well illustrates certain features about Siphonaptera which apparently have not been noted before or else are not generally appreciated, viz., 1) Modification of the head for maintenance of a semi-sedentary position. 2) Modification of the pronotal comb in a way believed to be characteristic of fleas of mammals which are both nocturnal and arboreal; and what may be termed 3) the Principle of Totality of Mass and 4) the Principle of Structural Compensation. These are discussed below, along with 5), a note on sibling species.

1) *Modifications of the Head.* Attention has been called to the flattened frontal margin of the head of certain pygiopsyllid fleas (Traub, 1968), i.e., *Idiochaetus* Jordan, 1937, *Ernestinia* Smit, 1953, *Striopsylla rugatus* (Jordan, 1937) and helmeted fleas like some *Stephanocircus* Skuse, 1893 (Stephanocircidae), etc., and it was prognosticated that these fleas press the head against the skin of the host

and hook the adjacent (and flattened or coarse) hairs by means of their spines or spiniform bristles. *Muesebeckella* has a head of this type, and it was noted while collecting those specimens which had remained on the host, that the fleas were indeed affixed to the hairs in this way. However, insufficient numbers of *Muesebeckella* have been found to date to determine if this behavior is really characteristic. It is therefore noteworthy that during this field-trip in New Guinea we collected hundreds of *Idiochaetis* from giant-rats and large numbers of *Striopsylla vandeuseni* Holland, 1969, from bandieoots and carefully observed the behavior of the fleas on the active or partially anesthetized host. Fleas of both genera were frequently noted to have the flattened head abutted against the skin of the host, and oftentimes some or all of the legs were dangling. The attachment via the spiniforms in *Idiochaetis* was so effective that the only way the fleas could readily be extricated from the host by means of forceps was to first pull the flea forward to release its hold, or else to pull the insect along the hairs to their extremities. Forcibly removing the fleas backwards often led to damaging or breaking the specimens. Unlike the case of ordinary fleas, which run about amongst the hairs of the host, anesthetizing or spraying the host while it was in a cloth bag did not result in large numbers of *Idiochaetis* or *Striopsylla* fleas dropping from the mammal. It was necessary to brush the fur vigorously (against the "grain") to collect the specimens, or else search for them individually.

It seems probable that the leathery or relatively untanned upper portion of the frontal margin of *Muesebeckella* is likewise an adaptation to enable the flea to secure (maintain) its position on the host. Thus, a pliable surface would be more apt to follow the contour of the skin when the flea firmly pressed its head against the body of the host. I also believe that the rugose cuticle of the head of *Muesebeckella*, *Ernestinia* and *Striopsylla* is similarly adaptive.

The flattened condition of the head is further discussed in 3) below.

2) *The Pronotal Comb.* It is well known that bird-fleas possessing a pronotal comb have more spines in the comb than do their relatives infesting rodents, i.e., 24-30 spines versus 18-22, and that the spines in the ctenidium of the former are also significantly narrower than those of the latter (Traub, 1950; Hopkins, 1957; Smit, 1958; Holland, 1964; Traub & Barrera, 1966). By these criteria, it would be expected that *Muesebeckella* was in reality a bird-flea, but this is manifestly not the case—all known specimens are from a small species of *Pseudochirus* despite the fact that hundreds of birds and thousands of mammals were examined by the Bishop Museum teams in New Guinea. (The validity of the observation regarding the host of *Muesebeckella* is indicated further by the facts that the birds yielded another

new genus of flea and two new species of *Hoogstraalia* Traub, 1950, while the common, large *Pseudochirus* was always free of fleas or else carried a few *Pulex irritans*.) There are at least three other characteristic features of the combs of bird-fleas which presumably have not been reported before, namely: a) the axis of the lower part of the comb slopes anteroventrad, whereas in the related mammal-fleas an imaginary line connecting the bases of the spines would be vertical. b) The comb itself does not extend ventrad so as to overlap the coxa. The multiplicity of spines occurs on a comb which is no broader (taller) than that of the mammal-fleas, and this is accomplished by the reduction in the breadth of the individual spines. c) The spines themselves are straight and horizontal, paralleling the longitudinal axis of the flea, and apparently also are of more uniform breadth throughout than in the rodent-fleas, which taper more, at least subapically. These features are found in the nine genera of combed-fleas (representing three different families) which are known to me as parasitizing birds (the figures include one undescribed new genus from New Guinea and the first bird-infesting *Pygiopsylla*, a new species).

The comb of *Muesebeckella* (figs. 1, ♂; 2, ♀), by contrast, extends down over the vinculum linking the pronotum with the mesothorax, and its axis is arched, with the lower two-thirds curving ventrocaudad. Moreover, the lower spines are oblique in inclination, and most of them are slightly upcurved (dorsal margin slightly concave and ventral margin correspondingly convex). This is the type of comb that for some reason is characteristic of fleas of tree-living mammals that are nocturnal (Traub, 1966). The phenomenon will be discussed at length in another article. Suffice it for the present to indicate that, in my opinion, *Pleocheatis ponsi* Barrera, 1955, and *Pleocheatis smiti* Johnson, 1954, are in this category.

3) *The Principle of Totality of Mass.* There are several structures that vary in size or mass in different genera and species of Siphonaptera, and it is interesting that despite the variations in the components, the resulting size or mass of the structure is a "constant," within the overall limits of the configuration of the taxon involved. Examples of this phenomenon were cited by Traub & Evans (1967), i.e., fleas with a narrow pronotum have very long spines in the pronotal comb, while, in contrast, those possessing short spines have a long pronotum. The known species of *Muesebeckella* are in the former category, and an example of the latter is *Ceratophyllus hagaromo* Jameson & Sakaguti, 1959, while the genus *Brevictenidia* Liu & Li, 1965, gets its name from the vestigial spines in the pronotal comb, but, significantly, the pronotum itself is exceptionally long.

Another manifestation of this principle is exhibited by the fore-

shortened head of *Muesebeckella*. Here, as in *Sigmactenus* Traub, 1950, *Ernestinia*, *Idiochaetis*, *Stephanocircus*, *Striopsylla* and other fleas with a narrow frons, the volumetric capacity of the head is unchanged from that in related fleas with typical or "normal" heads because in the flat-headed fleas there is a corresponding increase in height. Further, in fleas with an evolutionary tendency toward prolongation of a vertical genal comb, the head becomes progressively narrow and tall as the number of spines increases, i.e., *Peromyscopsylla* I. Fox, 1939 (2 spines on a fairly broad head; ex cricetids), *Leptopsylla* Jordan & Rothschild, 1911 (3-6 spines on a fairly narrow head; ex cricetids and murids), *Pectinoctenus* Wagner, 1930 (7-14 spines on a narrow or very narrow head; ex murids); *Sigmactenus* (9-12 spines on a very narrow head; ex *Rattus* (*Rattus*).³ Interestingly enough, as the comb increases in height, the rudimentary eye of the flea assumes a more and more dorsal position, still staying associated with the first one or two spines, so that in *Sigmactenus* it is near the top of the head. (The migration of the eye with the comb provides proof that these vertical combs indeed are *genal* structures.)

The dimensions of the tibia also vary, but again in accordance with this principle. For example, the hind-tibia is unusually long and narrow in *Sigmactenus* but very short and broad in *Malacopsylla* Weyenbergh, 1881, and *Phthiropsylla* Wagner, 1939.

The variations from the ordinary or common type of structure always seem to result in a constant—no fleas are known to possess a head or tibiae which are both long *and* tall. The effect is as if there were a limit to the protein or tissue available for the end-product, regardless of what it might be. Since these variations in head, leg, etc., occur again and again in unrelated fleas and often skip the allied taxa, they constitute examples of convergence.

4) *The Principle of Structural Compensation* is a corollary of the foregoing in that it concerns concomitant variations in size, but in this case two (or more) separate structures are involved (instead of the dimensions of the same sclerite or organ), although the members of the pair or group presumably work together or have a common function. For example, in many fleas both the immovable and movable processes (P. and F.) of the clasper are essentially the same size, i.e., *Jellisonia klotzi* Traub, 1944. However, oftentimes F. is extremely large, as in *Muesebeckella* (fig. 11, F.) and at such times P. is correspondingly reduced. The converse is the case in *Chaetopsylla* Kohaut, 1903, where P. is massive. A similar phenomenon is to be noted in the sundry hooking or prying devices on the acdeagus. In certain

³ One reason for believing that the course of development in this group was from fewer spines to a greater number, is the geologic age of the various hosts; zoogeographic considerations constitute another. These are discussed by Traub et al. (in press).

groups of fleas, i.e., ceratophyllids and many leptopsyllids, the crochets, which are ventral, are huge (and often articulated), but Ford's sclerite, which is dorsal, is then reduced and hardly modified. In some leptopsyllids and many other fleas, including most pygiopsyllids, the reverse is true—Ford's sclerite is well developed and the crochets are small. In *Muesebeckella*, Ford's sclerite (fig. 10, F.S.C.) dominates the end chamber, and there is no true crochet, nor any other ventral "paramere." There are pygiopsyllids, i.e., *Parastivalius novaeguineae* (Rothschild, 1904), in which Ford's sclerite is not so well developed, and in which the crochet lacks a caudad-directed hook-like process, but here the ventral "paramere" is a bifid lobate structure (appearing distally paired and falcate as seen in the usual lateral position, but is actually scoop-like). This in reality is the highly modified ventral armature of the sclerotized inner tube, which is distal in position in this species and not at all like that seen in *Muesebeckella* (fig. 17, V.AR.). The end-result is the same—an elaborate and obviously effective device for copulation, even though different components are used.

The comparative size of the hood flaps and the lateral lobes of the aedeagus is also in accord with this principle. Thus, when the hood bears well developed flaps (figs. 17, 18, DEL.FL.), the lateral lobes are reduced, as in the *Stivalius robinsoni* group, or else inapparent, as in *Muesebeckella*. In the case of *P. novaeguineae*, the lateral lobes are much larger than the flaps of the hood, while in *Papuapsylla* Holland, 1969, the lateral lobes are extremely well developed at the apparent expense of the flaps of the hood.

The relative size of the abdominal terga and sterna well illustrate this principle, particularly in the case of the male eighth segment. Thus, while most of the genitalia is always effectively covered by the eighth segment, the means whereby this is effected varies considerably, generally depending upon the family or subfamily of the taxa involved. In pygiopsyllids, the eighth tergum (fig. 8, 8 T.) is greatly reduced, while the sternum (8 S.) is correspondingly enlarged, taking over most of the function of its puny "mate." (Interestingly enough, the opposite condition applies to the rest of the regular abdominal segments in this group, where the tergum extends down over most of the sterna, i.e., 7 T. and 7 S.) In ceratophyllids and ischnopsyllids, the situation is reversed, and it is 8 T. which is huge, while 8 S. is very small, or even vestigial. In leptopsyllids, 8 S. and 8 T. are frequently subequal in size, although in some instances (i.e., *Ophthalmopsylla* Wagner & Ioff, 1926) 8 S. becomes elongate and highly modified, and in those cases 8 T. is accordingly somewhat larger than usual.

The term compensation is used because of the hyperdevelopment of one structure to take over the function of one that has retrogressed

in the course of evolution. In a sense, these points are also examples of Dollo's Law in that once a structure has been lost, another must be modified to replace it, since the original cannot be "resurrected" (Traub, 1968).

5) *Muesebeckella mannae*, n. sp. and *M. nadi*, n. sp. represent a phenomenon that is notably relatively common amongst New Guinean Siphonaptera—that of the occurrence of sibling- or sister-species. Characteristically, the two species resemble one another closely, but upon critical study it soon becomes apparent that there are significant differences in morphological details, usually along the same lines as those noted for *Muesebeckella*, but at times also including variations in the pattern of pronotal spines, etc. (Traub, 1968).

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LIST OF ABBREVIATIONS USED IN ILLUSTRATIONS

A.B., antepygidal bristles. A.G., apical group of dorsolateral marginal tibial bristles. A.S., anal stylet. AE.A., aedeagal apodeme. AE.F., fulcrum of aedeagus. ALPH., alpha-portion of securifer of Ford's sclerite. AN.GP., anterior group of marginal bristles on F. AP.R., third aedeagal rod (accessory aedeagal rod). B., bulga (head) of spermatheca. B.C., bursa copulatrix. B.CR., basal sclerite of crochet. B.M.L., bay of middle lamina. B.S.N., basal sclerotized notch of ♂ ninth sternum. C.P., conical process on anterior portion of P. C.S., crescent sclerite. CEN.S., central sclerite. D.A.L., dorsal anal lobe. D.A.9, distal arm of ninth sternum. D.B.C., duct of bursa copulatrix. D.FR., distal fringe of bristles on F. D.V., dorsal virga of aedeagus. D.VG., duplicatura vaginalis. D.SP., duct of spermatheca. DEL.FL., deltoid flap of hood of aedeagus. DM.1–DM.5, groups of dorsolateral tibial bristles arising from marginal notches. F., movable process or finger of clasper. F.S., fulcrum sclerite at base of attachment of F. F.SC., Ford's

sclerite. FUL.L.L., lateroventral lobes of fulcrum of aedeagus. FUL.M.L., median lobe of fulcrum. G., girdle of aedeagal pouch. G.V.G., glandula vaginalis. H., hillia (tail) of spermatheca. HD., hood of aedeagus. L.A., lower arm of securifer of Ford's sclerite. L.L., lateral lobes of aedeagus. LLAM., lateral lamina of aedeagal apodeme. L.M., lateral metanotal area. L.P., labial palpus. L.S.C., lateral shafts of capsule of aedeagus. M.D.L., median dorsal lobe of aedeagus. M.LAM., median lamina of aedeagal apodeme. M.P., maxillary palpi. MB., manubrium. MPM., mesepiphore. MPS., mesepisternum. MTM., metepiphore. MTN., metanotum. MTS., metasternum. P., immovable process of clasper. P.A.9, proximal arm of ninth sternum. P.B.C., perula of bursa copulatrix. P.R., penis rods. PHY., phylax of aedeagus. PIV.R., pivotal rod of aedeagus, terminating at Ford's sclerite. PLA., pleural arch. PS.S., pseudoseta(e). S.G., group of sensillae at anterodistal angle of F. S.I.T., sclerotized inner tube of aedeagus. S.S., subanal sclerite. SAT.S., satellite sclerite of capsule of aedeagus. SEC., securifer of Ford's sclerite. SP., spermatheca. SQ., squamulum. T.AP.9, tergal apodeme of ninth segment. T.L.S., tendons of lateral shafts of capsule. U.A., upper arm of securifer of Ford's sclerite. U.L.7, upper lobe of 7 T., above plate of antepygidal bristles. V., vesicle. V.A.L., ventral anal lobe. V.AR., ventral armature of sclerotized inner tube. V.V., ventral virga of aedeagus. VC.1, first vinculum or link-plate. Y.S., Y-sclerite of capsule. 1 T., first tergum. 7 S., seventh sternum. 8 S., eighth sternum. 8 SPC., spiracular fossa of eighth segment. 8 T., eighth tergum. 9 S., ninth sternum.

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